ASPECTS OF THE LIFE HISTORY OF THE FLUFFY SCULPIN, *OLIGOCOTTUS SNYDERI*

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ABSTRACT

We examined age structure, growth rates, and diets of male and female *Oligocottus snyderi* Greeley at Dillon Beach, CA, where this sculpin numerically dominates the mid- and lower intertidal fish assemblage. Two age classes, 0+ and 1+, were present; maximum lifespan was about 1.5 years. Instantaneous population growth rates were highest for the 0+ age class, and most individuals attained spawning size during the first year of life. Growth rates for both age classes were highest during the high productivity Upwelling period and minimal during the low productivity, Oceanic-Davidson Current period.

Males and females primarily consumed gammarid amphipods and polychaetes. Larger individuals (≥50 mm SL) of both sexes consumed a wider variety of prey, including shrimps, crabs, and isopods. Among year and seasonal dietary changes were minimal. Females consumed two times more gammarids by weight than males during the low productivity Oceanic-Davidson Current period, when ovarian recrudescence occurs. Females may increase food consumption to meet the increased energetic demands of egg production.

Rapid sexual maturation and growth and the occurrence of recruitment during upwelling probably are adaptations to the pronounced annual cycle of productivity. These adaptations, together with intense utilization of an abundant prey (gammarids) not widely consumed by other assemblage members, probably contribute to *O. snyderi*'s numerical dominance in the rocky intertidal of central California.

The fluffy sculpin, *Oligocottus snyderi* Greeley, is a common species which inhabits the rocky intertidal from Baja California to Sitka, AK (Miller and Lea 1972). Between central California and British Columbia, *O. snyderi* frequently is very abundant (Green 1971; Cross 1981; Yoshiyama 1981; Grossman 1982). This species occurs primarily in mid- and lower intertidal areas (Green 1971; Yoshiyama 1981), and often is associated with surfgrass (Green 1971; Nakamura 1976a). The general absence of this species from the high intertidal is probably due to its inability to tolerate higher temperatures which frequently occur in high intertidal pools (Nakamura 1976b).

Life histories of intertidal fishes, particularly cottids, are poorly known (Gibson 1969, 1982). Published information on the demography of *O. snyderi* is restricted to the work of Moring (1981), who examined age structure of a northern California *O. snyderi* population, and Grossman and deVlaming (1984), who described the species' reproductive ecology. This paper presents data on age structure, growth rates, and dietary habits of an *O. snyderi* population at Dillon Beach, CA, a site that is subject to pronounced annual cycles of oceanic productivity (Parrish et al. 1981). *Oligocottus snyderi* numerically dominates the intertidal fish assemblage at Dillon Beach (Grossman 1982); the present study explores demographic and ecological characteristics which may account for this species' ecological success in the rocky intertidal.

MATERIALS AND METHODS

Collections

Oligocottus snyderi were collected from a series of mid- and lower intertidal pools at Dillon Beach, CA, on 15 dates from January 1979 to July 1981 (see Grossman in press a for sampling dates). Repeated collecting did not affect assemblage structure (Grossman 1982, in press a). Fish were obtained by spreading a 10% solution of quinaldine in isopropanol through the pools and then collecting individuals after anesthetization. Over 1,400 *O. snyderi* were collected. Specimens were preserved in buffered Formalin[3] and were later washed and transferred to 45% isopropanol. Individuals were measured to the nearest millimeter standard length (SL) and weighed to the nearest 0.1 g. Sexes of all

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individuals collected during 1979 and of specimens used for gut analysis also were recorded. A complete description of collecting methods and the study site are presented in Grossman (1982, in press b).

Collection dates were assigned either to the Upwelling or the combined Oceanic-Davidson Current (ODC) oceanographic seasons, based on water temperature and a calculated upwelling index (see Grossman in press b). The Upwelling period is characterized by frequent upwelling of nutrient-rich waters and high productivity (Bolin and Abbott 1963; Garrison 1979). In contrast, the ODC period exhibits minimal upwelling, frequent downwelling, and low productivity (Bolin and Abbott 1963; Garrison 1979). Data from individuals collected during the latter seasons were pooled because these periods were not readily distinguishable (Grossman in press b). Consequently, comparisons of *O. snyderi* food habits and length-weight relationships represent contrasts between a high productivity period (Upwelling, all months from April to August, plus March 1980) and the low productivity ODC period (October-February, plus March 1979). Monthly mean water temperatures ranged from 9.7° to 11.9°C during the Upwelling period from 11.2° to 14.2°C during the ODC period (Grossman in press b).

Length-Weight and Growth Calculations

Regressions of individual weight versus standard length were calculated separately for males and females collected in the Upwelling and ODC periods. Regression equations were of the form $W = aL^b$, fitted as $\ln W = \ln a + b \ln L$. Slopes (b) of regression equations for males and females were compared for each period by analysis of covariance (ANCOVA). Seasonal differences between slopes also were examined for each sex.

Regression slopes for the two sexes and periods were divided by their correlation coefficients to estimate slopes for geometric mean functional regressions of weight versus length (Ricker 1973). Functional regressions are recommended for describing relations between weight and length because both variables are subject to natural variability (Ricker 1973). Functional regression slopes were used to derive y-intercepts from the equation $y\text{-int.} = \bar{y} - (b/r)\bar{x}$ (Ricker 1973). These slope estimates were employed to calculate instantaneous rates of growth in weight (G) as

$$G = (b/r)\ (\ln L_2 - \ln L_1),\ \text{(Ricker 1975)},$$

where b/r = slope of the functional length-weight regression;

L_1 = mean length at the time t; and

L_2 = mean length at time $t + 1$.

Growth rates were calculated for individual year classes which were separated using length-frequency distributions. To compare growth rates for males and females, t-tests for paired samples were used.

Sex ratios for the 1979 samples were tested for deviations from unity using chi-square tests corrected for continuity.

Dietary Analyses

Stomach contents were removed from a subsample (597 total) of the *O. snyderi* collected between January 1979 and July 1981. Ninety-seven percent of stomachs examined contained food. Prey were identified to the lowest possible taxon and weighed (wet) to the nearest milligram. The weights of each prey type were pooled separately for males and females from each collection. Diets were then calculated as the percent of the total stomach content weight attributable to each prey type. The number of fish containing each prey type (i.e., prey frequency of occurrence, henceforth FO) also was recorded.

Dietary data were pooled across collections within the Upwelling and ODC periods for each sex, to compare feeding habits between sexes and seasons. Because the study period spanned 3 yr, it also was possible to quantify among year variability in seasonal and sex-specific feeding habits. Sex-linked ontogenetic dietary changes were examined by separating males and females into 20 mm size classes and comparing prey consumed by each size class in different seasons and years. Niche breadth was calculated as $\Sigma\ 1/p_i^2$ (Levins 1968), where p_i is the proportion of the total prey weight comprised of the ith prey type. Only prey types constituting at least 1% of the total prey weight were included in niche breadth calculations. Niche breadth was compared among size classes by using the Wilcoxon signed-rank test.

RESULTS

Length-Weight Relationships

The slope for the male length-weight regression for the Upwelling period was significantly greater than that for females (ANCOVA, $F = 12.875$, $P < 0.001$; Table 1). Slopes of length-weight regressions for males and females collected during the ODC period were not significantly different (ANCOVA,

TABLE 1.—Length-weight relationships, described as $W = aL^b$, for *Oligocottus snyderi*. Coefficients for the least-squares (ln W = ln a + b ln L) and functional (ln W = ln a' + (b/r) ln L) regressions are presented, as well as the correlation coefficients for the least-squares regressions (r) and the number of individuals used in each regression (N). ODC = Oceanic-Davidson Current.

			Least-squares regression		Functional regression	
	N	*r*	*a*	*b*	*a'*	*b/r*
Males						
Upwelling	150	0.984	0.0000178	3.097	0.0000146	3.147
ODC	112	0.973	0.0000253	2.991	0.0000182	3.075
Females						
Upwelling	164	0.972	0.0000472	2.835	0.0000346	2.917
ODC	131	0.976	0.0000202	3.069	0.0000151	3.143

$F = 0.736$, $P > 0.25$). Seasonal comparisons for each sex showed that the male Upwelling and ODC slopes were not significantly different (ANCOVA, $F = 1.483$, $P > 0.10$), whereas the females had a significantly higher slope during the ODC period (ANCOVA, $F = 6.147$, $P < 0.025$).

Growth Rates

Length-frequency histograms for *O. snyderi* at Dillon Beach indicated that two year classes were present on most dates (Fig. 1). Recruitment began in spring and peaked during summer. The onset of recruitment differed between years. Age 0+ fish were first taken in May of 1979; however, in 1980 recruitment began in March. Age 0+ individuals of the 1979 cohort grew 20 mm in length (from 20-25 to 40-55 mm SL) by December of their first year. Members of the 1978 cohort (= age 1+ fish) increased in length from 40-55 to 60-70 mm SL during spring, summer, and fall 1979. Individuals did not appear to survive a second winter during 1980, although a few males recruited in 1977 may have survived until spring of 1979 (Fig. 1).

Sex ratios for the 0+ age class were significantly different from unity in the August 1979 collection in which there were significantly more males than females (1.7:1; $\chi^2 = 7.32$, $P < 0.01$). Age 1+ females significantly outnumbered males in January 1979 (4:1; $\chi^2 = 6.05$, $P < 0.025$), July 1979 (1.8:1; $\chi^2 = 4.38$, $P < 0.05$), and December 1979 (3:1; $\chi^2 = 5.04$, $P < 0.025$).

Instantaneous growth rates were calculated for males and females from the two year classes present in 1979 (Table 2). Prolonged recruitment (lasting from May through August) resulted in apparent depressed spring and summer growth rates for the age 0+ class when all individuals were included in the calculations of mean lengths (Table 2). Therefore, fish which appeared to have been recruited later than the majority of the class were excluded from consideration in the June, July, and August calculations, as shown in Figure 1. Only the very large males collected in January 1979 were excluded from the age 1+ mean length calculations, as these individuals apparently were survivors from the 1977 year class and probably died shortly thereafter. The highest monthly instantaneous growth rates were obtained during May and June, averaging 0.860 and 0.655 for age 0+ males and females, and 0.209 and 0.188 for age 1+ males and females (Table 2, Fig. 2). Growth rates markedly decreased after August, averaging 0.065 and 0.169 for age 0+ males and females, and 0 and 0.061 for age 1+ males and females during October and November (Table 2, Fig. 2).

Males and females attained nearly equal lengths in the first season of growth; however, age 1+ males displayed significantly greater mean lengths (t-tests, $P << 0.05$) than age 1+ females from June through November 1979 (Fig. 2). Growth rates were not significantly higher for males than females in either size class when compared from January to December 1979 (age 0+: $t = 1.002$, $P > 0.1$; age 1+: $t = 1.232$, $P > 0.1$); however, if only the data from January to October are included for the age 1+ class, males did have significantly higher growth rates ($t = 2.255$, $P < 0.05$). This discrepancy is caused by the low numbers of age 1+ fish collected in November (14) and December (24). Length-frequency histograms (Fig. 1) also show that age 1+ males are larger than females, whereas length distributions are

TABLE 2.—Instantaneous growth rates of *Oligocottus snyderi* males and females in their first (age 0+) and second (age 1+) years of growth. Rates were calculated for the intervals between the 1979 collections. Values in parentheses were calculated with all individuals included in the age 0+ cohort (see text).

	Instantaneous growth rate			
	Age 0+		Age 1+	
Collection dates	Males	Females	Males	Females
1-27-79				
	—	—	0.257	0.079
3-26-79				
	—	—	0.295	0.171
5-16-79				
	1.059 (1.059)	0.718 (0.562)	0.318	0.204
6-13-79				
	0.661 (0.429)	0.591 (0.358)	0.099	0.171
7-12-79				
	0.352 (0.306)	0.295 (0.390)	0.111	0.074
8-09-79				
	0.303 (0.582)	0.124 (0.419)	0.164	0.063
10-07-79				
	0.129	0.149	0	0.122
11-04-79				
	—	0.188	—	—
12-04-79				

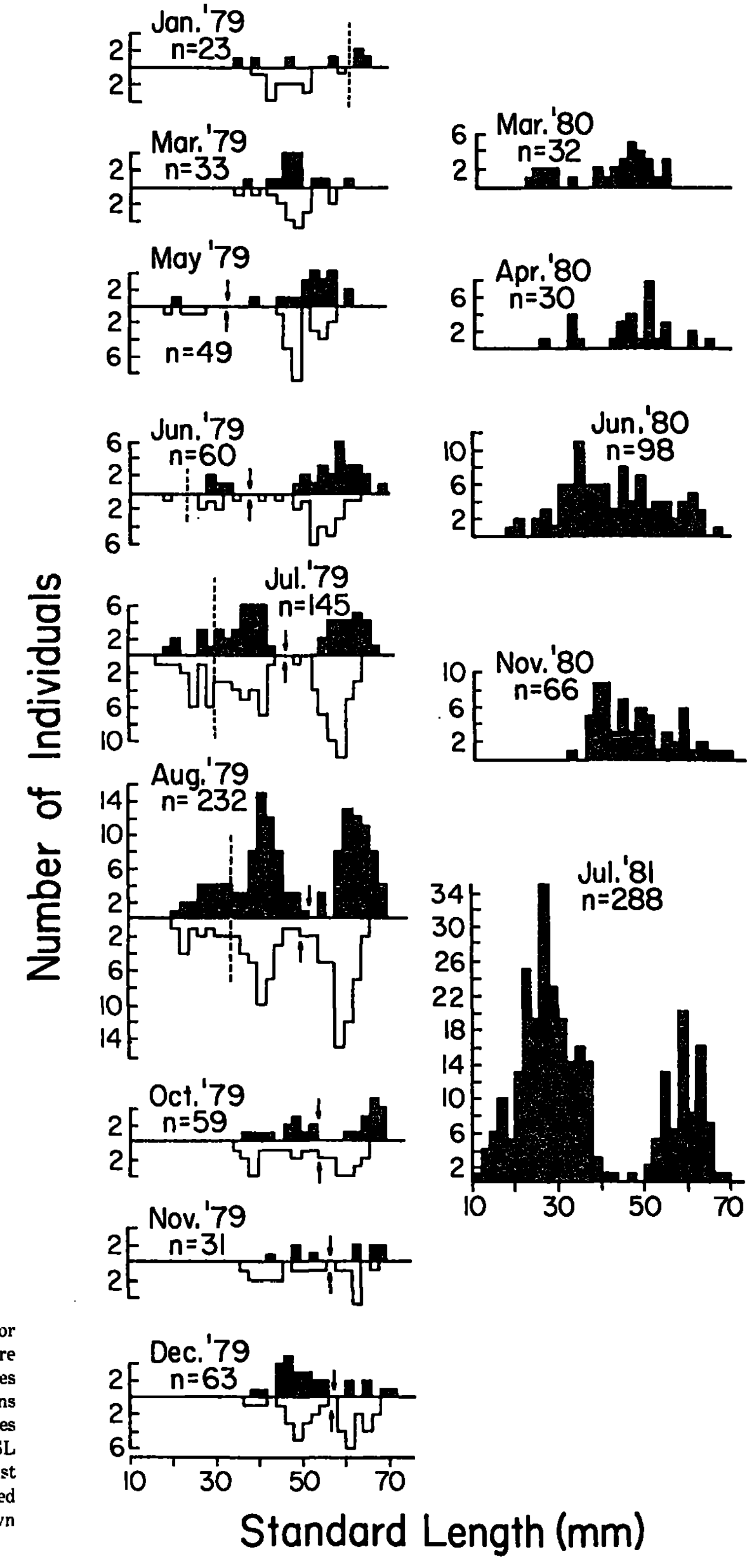

FIGURE 1.—Length-frequency distributions for *Oligocottus snyderi*. Males and females are separated in the 1979 collections, with females shown below the axis. Arrows indicate divisions between year classes 0+ and 1+, and broken lines designate limits for inclusion in cohort mean SL calculations (January, June, July, and August 1979). The 1980 and 1981 collections are included for comparison, but the sexes are not shown separately.

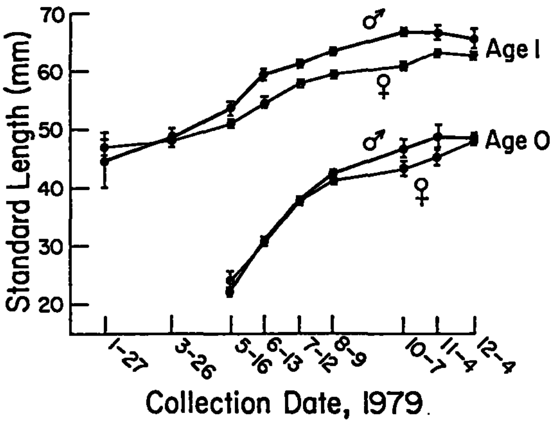

FIGURE 2.—Growth curves for age 0+ and 1+ *Oligocottus snyderi*. The standard lengths ($\bar{x}$ ± SE) of each sex in the two age classes are shown for the 1979 collections. June, July, and August age 0+ SLs do not include late recruited individuals (see text and Figure 1).

about equal for age 0+ males and females. The low mean lengths calculated for age 0+ females in October and November resulted from the inclusion of small individuals probably recruited late in Upwelling, but which were not easily separable from the remainder of the cohort. Hence, calculated growth rates probably underestimate age 0+ female growth from August to October and overestimate growth from October to December.

Dietary Habits

Oligocottus synderi's diet at Dillon Beach consisted primarily of gammarid amphipods and polychaetes. Summed across all collections, gammarids composed 78% and 66% of the gut contents of females and males, respectively. Polychaetes totaled 10% of the female diet and 14% of the male diet. Shrimp remains, mainly *Heptacarpus taylori*, contributed 5% and 4% to female and male diets, respectively. A total of 20 prey taxa were consumed by *O. snyderi*; however, no other prey category composed more than 3% of the diet, with the exception of unidentifiable hard-bodied prey remains, which totaled 5% of the gut contents of males. Dietary breadth based on all collections was higher for males than females (2.17 vs. 1.61), because males consumed greater amounts of minor prey types.

The major seasonal dietary changes for both males and females were decreased gammarid consumption and increased polychaete consumption during Upwelling as compared with the ODC period (Tables 3, 4). Dietary breadth also was greater for both sexes during Upwelling than in the ODC period (2.02 vs. 1.44 for females, and 2.19 vs. 2.09 for males). Differences were observed between male and female diets. Specifically, in the ODC period, gammarids composed a greater proportion of female than male diets (83% vs. 68%), whereas males consumed proportionately more eggs, *Idotea* spp. (Isopoda), and crabs (Table 4). Although standard lengths and weights of ODC males (138) and females (132) used for gut analyses were not significantly different (SL: $t = 1.058, P > 0.1$; weight: $t = 1.036, P > 0.1$), females had significantly greater amounts of food in their stomachs ($t = 4.857, P = 0.0001$, Table 4). This difference is attributable to the weight of ingested gammarids because 131 (FO) females contained a total of 8.4 g of gammarids, whereas 132 males contained only 4.3 g (total weight).

Examination of food habits across size classes shows that larger individuals generally possessed a more diverse diet than smaller individuals (Figs. 3, 4). Dietary breadth was significantly higher (Wilcoxon signed-rank test, $n = 12, T = 69, P < 0.01$) for 50-69 mm SL fish than for 30-49 mm SL individuals when compared across both sexes for all years. Individuals <30 mm SL consumed mainly gammarids and isopods; polychaetes and shrimp were major prey only for larger fish. *Pagurus* spp. and crabs, including *Cancer* spp. and *Pachycheles* spp., were found only in individuals ⩾40 mm SL.

The general observation of decreased gammarid consumption by larger *O. snyderi*, concomitant with increased polychaete and shrimp consumption, applies to collections made throughout the 3-yr study period. The majority of among year variation in food habits resulted from the presence of large, rare prey items in single individuals (Figs. 3, 4). An exception was the high consumption of polychaetes by males collected in July 1981 (Fig. 3). In this case, polychaetes occurred in all of the 50-69 mm fish and in 56% of the 30-49 mm fish, and composed a considerably higher proportion of the diet than during previous Upwelling collections.

DISCUSSION

Age-Structure and Growth

At Dillon Beach, a habitat displaying marked seasonal fluctuations in productivity (Grossman 1982, in press b; Grossman and deVlaming 1984), *O. snyderi* is short lived, with a maximum lifespan of about 1.5 yr and a maximum length of about 70 mm SL. Whereas two age classes were observed in this study, Moring (1981) observed as many as three age classes in Trinidad Bay. Standard lengths attained

TABLE 3.—Food habits of male and female *Oligocottus snyderi* collected during the Upwelling period. Values shown for each prey type are total weight ingested, percent of total prey weight, and frequency of occurrence (FO).

$\bar{x}$ SL ± SD	Females, *n* = 164 45.9 ± 11.7 mm			Males, *n* = 150 51.3 ± 11.8 mm		
Prey	Wt. (g)	% Wt.	(FO)	Wt. (g)	% Wt.	(FO)
Gammarids	3.850	68	(125)	3.653	64	(132)
Polychaetes	0.980	17	(19)	1.109	19	(33)
Heptacarpus taylori	0.202	4	(4)	0.222	4	(5)
Crangon	0.146	3	(2)	0		
Other shrimp	0.001	<1	(1)	0.004	<1	(1)
Hard-bodied prey rem.	0.196	3	(18)	0.494	9	(20)
Isopods	0.095	2	(10)	0.074	1	(19)
Idotea	0.006	<1	(2)	0.049	1	(3)
Pagurus	0.067	1	(1)	0		
Crabs	0.036	1	(2)	0.026	<1	(1)
Algae	0			0.039	1	(9)
Snails	0.024	<1	(4)	0.010	<1	(3)
Caprellids	0.026	<1	(1)	0.004	<1	(2)
Soft-bodied prey rem.	0			0.014	<1	(1)
Barnacle cirri	0			0.012	<1	(5)
Total	5.629	99		5.710	99	

TABLE 4.—*Oligocottus snyderi* feeding habits during the combined Oceanic-Davidson Current periods. Values shown for each prey are the weight ingested, percent of total prey weight, and frequency of occurrence (FO).

$\bar{x}$ SL ± SD	Females, *n* = 132 49.5 ± 8.8 mm			Males, *n* = 138 50.6 ± 9.3 mm		
Prey	Wt. (g)	% Wt.	(FO)	Wt. (g)	% Wt.	(FO)
Gammarids	8.418	83	(131)	4.278	68	(132)
Polychaetes	0.611	6	(20)	0.587	9	(23)
Heptacarpus taylori	0.304	3	(3)	0.308	5	(4)
Crangon	0.089	1	(2)	0		
Other shrimp	0.071	1	(1)	0		
Eggs	0.008	<1	(1)	0.397	6	(6)
Idotea	0.131	1	(6)	0.252	4	(14)
Isopods	0.255	3	(19)	0.104	2	(16)
Sea anemones	0.147	1	(2)	0		
Hard-bodied prey rem.	0.053	1	(2)	0.086	1	(4)
Pachycheles	0			0.091	2	(1)
Barnacle cirri	0.001	<1	(1)	0.075	1	(5)
Pagurus	0.043	<1	(2)	0		
Bivalves	0			0.036	1	(1)
Algae	0			0.044	1	(9)
Caprellids	0.015	<1	(2)	0.003	<1	(1)
Cancer	0			0.005	<1	(1)
Crabs	0			0.002	<1	(1)
Snails	0.002	<1	(1)	0		
Total	10.148	100		6.268	100	

by the 0+ and 1+ age classes observed by Moring (1981) were similar to those displayed by the Dillon Beach age 0+ and 1+ classes; however, Moring observed age 2+ individuals of up to 101 mm SL. Nakamura (1976a, b) also reported collecting *O. snyderi* >80 mm SL at Port Renfrew, British Columbia. These results indicate that *O. snyderi* may have a longer lifespan at more northerly locations. The scarcity of individuals >70 mm SL at Dillon Beach probably did not result from repeated sampling because such large individuals were absent from the initial samples and from collections made in previously unsampled pools near the study site in August 1979, December 1979, and April 1980. There was no discernable pattern in sex-ratio deviations from unity observed in four 1979 collections, which

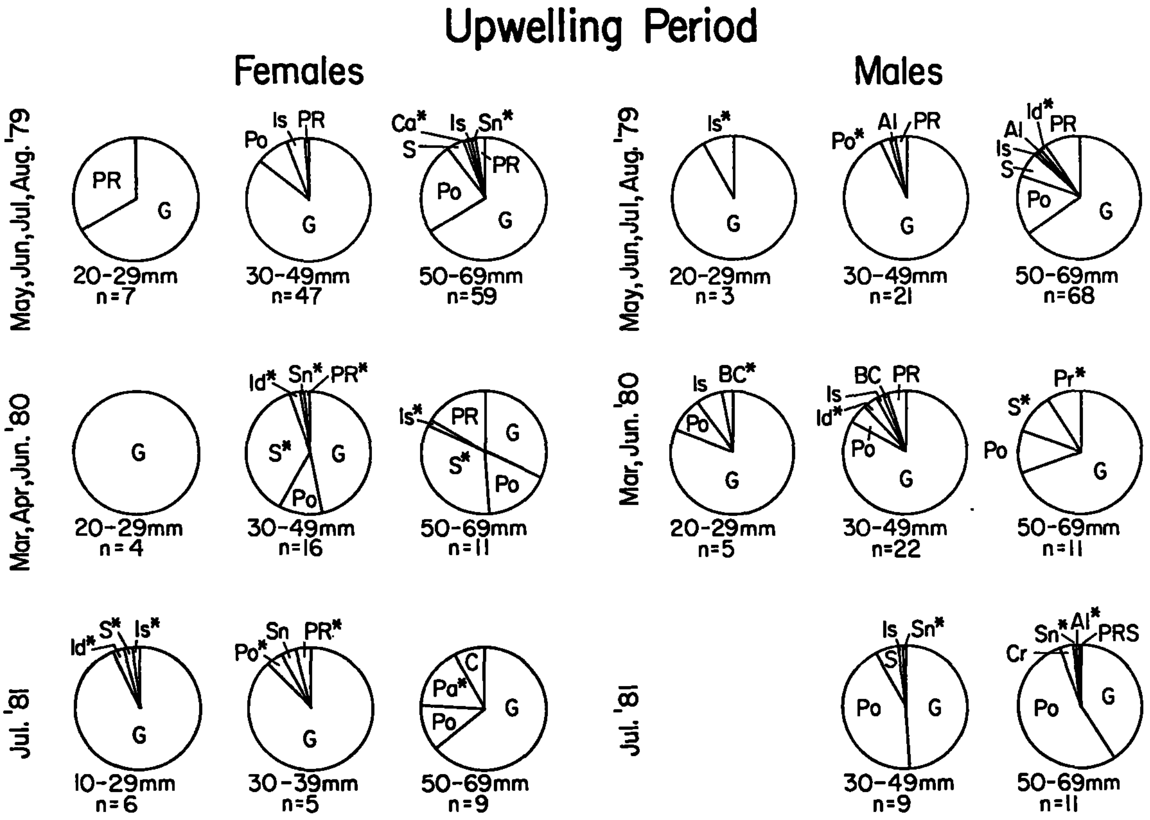

FIGURE 3.—Sex-specific ontogenetic and among year variation in *Oligocottus snyderi* feeding habits during the 1979, 1980, and 1981 Upwelling periods. Prey are represented as percent total prey weight, and only prey composing ≥1% of the total prey weight are shown. Asterisks indicate prey which occurred in only one individual. Prey abbreviations are G (gammarids); PR (hard-bodied prey remains); Po (polychaetes); Is (isopods); S (shrimps, all spp.); Ca (caprellids); Sn (snails); Id (*Idotea* spp.); Pa (*Pagurus* spp.); Cr (crabs, all spp.); Al (algae); and BC (barnacle cirri).

suggests that males and females have about equal lifespans at Dillon Beach.

Oligocottus maculosus Girard, another abundant intertidal cottid (Nakamura 1976a, b; Moring 1981), was estimated by Chadwick (1976) to survive as many as five growing seasons, based on counts of vertebral rings, at Port Renfrew, B.C., and Bruels Point, CA. Annuli were not validated in this study, however, and it is questionable if the rings observed were actually formed once yearly. In addition, Chadwick's (1976) growth rate estimates are extremely low, suggesting that *O. maculosus* grew no more than 7 mm in any season after the first. Moreover, all previous studies of both *O. snyderi* (Moring 1981) and *O. maculosus* (Atkinson 1939; Green 1971; Moring 1979) showed that populations of these species were composed primarily of age 0+ and 1+ individuals, as was *O. snyderi* at Dillon Beach. Consequently, it appears unlikely that *O. maculosus* survives to age 5+ as suggested by Chadwick (1976), and in any case such longevity was not observed for *O. snyderi* at Dillon Beach.

Intertidal fishes appear to display several distinct life history patterns. Short lifespan (1-3 yr), early maturation, and high reproductive effort have been reported for several intertidal gobies in northern temperate habitats (Gibson 1969, 1982; Grossman 1979; Miller 1979). In contrast, lifespans of 4 to over 10 yr, accompanied by delayed maturation, have been observed in many intertidal species, including gobiids and blenniids (Gibson 1969, 1982; Stephens et al. 1970; Grossman 1979; Miller 1979). Little information is available for intertidal cottids. The largest North American cottid, *Scorpaenichthys marmoratus* Ayers, may live 13 yr, but only inhabits tidepools during its first or second year of life (O'Connell 1953; Grossman and Freeman unpubl. data). Another large sculpin, *Leptocottus armatus* Girard, common in the Pacific coast bays and estuaries, is known to live to age 3 and reaches sexual maturity

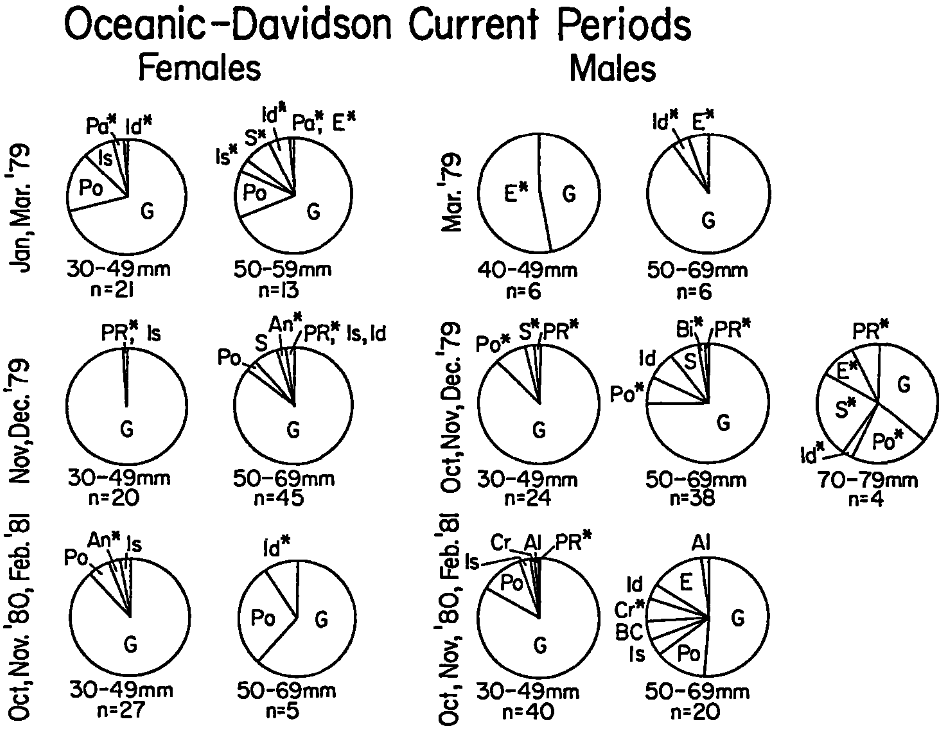

FIGURE 4.—Sex-specific ontogenetic and among year variation in *Oligocottus snyderi* feeding habits during the three ODC (Oceanic-Davidson Current) periods encompassed by this study. Prey are represented as percent total prey weight; only prey composing ≥1% total prey weight are shown. Asterisks indicate prey occurring in only one individual. Abbreviations are as in Figure 3, with the addition of E (eggs); An (sea anemones); and Bi (bivalves).

after 1 yr (Jones 1962; Tasto 1975). *Oligocottus snyderi* and *O. maculosus* apparently are best characterized by the short lifespan, early maturation, life history pattern. This conclusion is based on growth rate data coupled with the scarcity of individuals older than 1.5 yr, and data showing early maturation and high reproductive effort for *O. snyderi* (deVlaming et al. 1982).

The majority of age 0+ *O. snyderi* at Dillon Beach attained sufficient size to spawn during their first year; it is less certain what proportion of these individuals survive to spawn in their second year. Grossman and deVlaming (1984) indicated that, at Dillon Beach, females mature at about 40 mm SL and contain vitellogenic oocytes from October through May. These females also probably spawn more than once, primarily during winter and spring (Grossman and deVlaming 1984). Length-frequency distributions from March and May 1979 and March and April 1980 show that a single age class dominated the population. Hence, assuming that recruitment primarily was derived from this population, age 1+ individuals (recruited the previous spring and summer) must have been responsible for nearly all spring spawning. The paucity of large individuals (i.e., >60 mm SL) in winter or spring samples indicates that if individuals spawned in their second year, this reproduction must have occurred prior to January. Substantial numbers of age 1+ individuals were captured from October to December 1979 and in November 1980. Although the earliest recruitment observed at Dillon Beach occurred in March 1980, Moring (1981) captured newly recruited individuals as early as January. This suggests that fall spawning may occur in more northerly populations of *O. snyderi*.

Reproduction apparently is timed to insure that larvae metamorphose during upwelling. Grossman (1982) found a significant correlation between upwelling activity and the number of resident species with young-of-the-year present at Dillon Beach. Grossman and deVlaming (1984) also observed that *O. snyderi* recruitment was strongly correlated with productivity; the authors pointed out that the early recruitment observed in March 1980 coincided with the onset of upwelling, whereas both recruitment and upwelling were delayed until May 1979.

If some individuals do survive to reproduce during their second year, the larger sizes attained by males during their second growing season may be advantageous during spawning. This is because male *O. snyderi* have a lengthened and prehensile first anal ray with which they clasp females during copulation, and the larger a male is in relation to a female, the more efficiently he will be able to clasp her (Morris 1956).

Dietary Habits

Oligocottus snyderi at Dillon Beach consumed primarily gammarid amphipods and polychaetes. These data are consistent with previous observations (Johnston 1954; Nakamura 1971; Yoshiyama 1980), although they differ somewhat from results obtained by Cross (1981) from two sites in northern Washington. Cross (1981) reported that harpacticoid copepods were a major prey for *O. snyderi* at one site; similarly, polychaetes also were consumed only at one site. However, Cross (1981) also observed high gammarid consumption by *O. snyderi*, as well as by most other intertidal species he studied. In addition, gammarids have been cited as a major prey in other intertidal fish assemblages (Mitchell 1953; Johnston 1954; Zander 1979, 1982; Grossman in press b). At Dillon Beach, gammarids frequently were consumed by resident and seasonal intertidal fishes, although only one other resident (*Apodichthys flavidus* Girard) possessed a diet dominated by gammarids (Grossman in press b). Among year, seasonal comparisons, however, show that a variety of minor prey types also are consumed by *O. snyderi*.

Combinations of shrimps, crabs, hermit crabs, *Idotea*, and other irregularly consumed prey constituted a considerable proportion of *O. snyderi*'s diet throughout the year. This was particularly evident in larger fish, which suggests that capture of these prey is either more difficult for small fish due to morphological, physiological, or behavioral constraints, or involves increased predation risk. Similarly, a shift from gammarids to larger prey concomitant with increasing length was observed for the majority of intertidal fishes at Dillon Beach (Grossman in press b), and for some species studied by Cross (1981). In contrast, Yoshiyama (1980) was unable to detect dietary differences between small and large *O. snyderi*, or two other intertidal cottids. Yoshiyama pooled small samples collected throughout a year, however, which may have obscured seasonal changes in prey consumption. Because his samples were small, Yoshiyama also may have underestimated consumption of rare prey.

Although seasonal dietary changes were minor, there is evidence that females possessed higher ingestion rates than males during the ODC period. During this season of lowered productivity, females consumed two times more gammarids (by weight) than males, although mean fish length and gammarid frequency of occurrence were nearly identical between sexes. This difference between consumption rates may not be artifactual. Females develop and carry vitellogenic eggs during this period (Grossman and deVlaming 1984), and consequently have high energy demands. There was no evidence that intersexual or ontogenetic dietary differences resulted from differential distribution or collection disturbance.

The high prey weight observed in males and females collected during the ODC period is of interest in light of the low growth rates observed during winter months. Moring (1979, 1981) also observed cessation of growth during winter for both *O. snyderi* and *O. maculosus* in northern California. He suggested that reduced foraging activity caused by increased wave action during winter might partially explain this growth reduction. Dietary data from Dillon Beach do not support this conclusion because ODC specimens contained a greater total weight of prey than individuals collected during Upwelling, even though a greater number of individuals were examined during the latter period. The Dillon Beach study site probably is more sheltered from winter storm activity, however, than the Trinidad Bay sites observed by Moring (Grossman pers. obs.). In the absence of ingestion rate data for both seaons, results based on gut content weight alone are equivocal. Moring (1981) also suggested that gonadal development during the winter months might be responsible for reduced growth; this could also apply to *O. snyderi* at Dillon Beach.

In conclusion, *O. snyderi* the most abundant intertidal cottid at Dillon Beach, possesses a suite of characteristics which suggest that productivity has influenced the biology and behavior of this species. For example, *O. snyderi* reaches sexual maturity during its first year of life, and spawns at a time which enables recruitment to take place during the season of highest productivity (i.e., Upwelling (Grossman and deVlaming 1984)). Grossman (1982, in press b) presented strong evidence that productivity cycles also affect many other species at Dillon Beach, because this assemblage appears to be organized through interspecific exploitative competition for food. Recuitment and numerical abundances within this assemblage also were strongly correlated with productivity (Grossman 1982). *Oligocottus snyderi* possesses a variety of adaptations (e.g., rapid maturation, high female reproductive effort, utilization of an abundant prey not widely consumed by other assemblage members) which probably are responsible for its numerical dominance in a fluctuating environment.

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